DISCUSSION AND CONCLUSIONS

The Forage Fish Diet Overlap project has made progress in addressing the hypothesis that "planktivory is the factor determining abundance of the preferred forage species of seabirds." We have attempted to show that forage fish feeding ecology could relate to the abundance of piscivorous seabirds impacted during the *Exxon Valdez* oil spill by examining fish food habits, prey partitioning, preferred prey items, diet overlap and potential competition from 1994-1996. We have described seasonal and interannual prey composition and diet overlap of 14 forage species, including pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasi*), Pacific sandlance (*Ammodytes hexapterus*), pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), sockeye salmon (*O. nerka*), Pacific cod (*Gadus macrocephalus*), Pacific tomcod (*Microgadus proximus*), prowfish (*Zaprora silenus*), northern smoothtongue (*Leuroglossus schmidti*), eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), threespine stickleback (*Gasterosteus aculeatus*), and Pacific sandfish (*Trichodon trichodon*). We have also compared prey fields and prey selection of juvenile pollock and herring in summer and autumn, 1995 and of juvenile herring, sandlance and pink salmon in summer, 1996. We have examined impacts of forage fish trophic interactions by comparing fish feeding in allopatric and sympatric aggregations. All of these aspects of feeding ecology can impact growth, survival and perhaps distribution, thereby affecting their availability as prey resource for seabirds.

This project has, however, been limited by several factors. It requires further information from Project 163A, Biomass and Distribution of Forage Species, which has not been completed. Therefore, we have not fully addressed the aspect of density dependent interactions based on forage fish school density and biomass. The scope of sampling was limited spatially (1994) and temporally (1995, 1996), methodology varied between years, little directed sampling of different types of forage fish aggregations was possible, and expensive and time consuming (but necessary) laboratory analysis was limited after 1994. Forage fish trophic interactions with jellyfish are a new area of investigation. Nonetheless, a number of findings from APEX and SEA have helped to focus fish dietary descriptions. Central pieces of information on fish biology from the APEX project include: different forage species within PWS are pelagic offshore or nearshore; habitats vary ontogenetically and seasonally; forage species abundance varies interannually; school size varies tremendously and both spatial and temporal distribution are uneven; fish aggregations are sometimes mono-specific in composition and sometimes multi-species/age class in composition. Central pieces of information on seabirds include: seabirds mainly feed nearshore; some travel long distances from colonies to familiar feeding areas; their fish prey species vary, and size, type and quality all are selected for; reproductive characteristics vary between colonies and in relation to prey type, quality and abundance.

When considering the relationship of forage fish feeding to their abundance and availability to seabirds, all of these pieces of the ecosystem puzzle are important. Directed sampling is needed to make specific diet/prey field comparisons among forage fish that opportunistic sampling from surveys cannot address. In lieu of such directed sampling, the Forage Fish Diet Overlap project has attempted to "salvage" sample sets from survey samples to examine similarity of species' diets and to examine the influence of species on one another's feeding, ie., evidence of competition. Changes in prey composition, changes in diet similarity, and feeding declines indicated that competitive trophic interactions do occur among forage species. All of the core objectives of the diet study have been met, providing information toward the unravelling of the trophic cascade that contributed to lack of seabird recovery. Principal findings include:

1. Most forage fish species were planktivorous during the six months sampled in 1994, with large and small calanoid copepods a consistent component of prey biomass. *Pseudocalanus*, *Neocalanus*/*Calanus* spp., and a succession of large calanoids were consumed throughout the season.

2. Small calanoid copepods were the predominant zooplankter available in both summer and autumn, 1995, but seasonal and depth-related differences in prey fields and in prey selection were found. Zooplankton densities (243 µm mesh, 20 m vertical tow) ranged from 1800-4200 organisms*m^{-3} in 1996.

3. Species' diets shifted to a variety of macrozooplankters in summer and autumn, but in different months.

4. Pacific tomcod and salmonids were the least planktivorous forage species, but piscivory was occasionally observed among other species. Cods were also more benthiphagous than other species.

5. Food webs were the most complex in June. Significant diet overlap and prey partitioning were commonly observed. Diet overlap between species pairs shifted monthly.

6. Herring and pollock diets overlapped the most consistently of all species pairs. Information on other species pairs is limited.

7. Interannual differences in diet were correlated with size for some species and not for others. Herring, tomcod, capelin, and pink and chum salmon diets differed each year in July, but sandlance and pollock diets were consistent between years.

8. Evidence for trophic competition was found through several avenues that indicate feeding was inhibited or altered. A) In autumn, 1994 and 1995, YOY herring and pollock consumed greater numbers of prey in allopatric aggregations than in sympatric aggregations. This observation could relate to the seasonal decline in prey abundance. In summer, 1996 food quantity and stomach fullness declined for sympatric herring, pink salmon and sandlance compared to allopatric fish. This observation may have been related to a trend for decreased zooplankton densities in areas of sympatric aggregations. B) In autumn, allopatric herring selected different prey than herring sympatric with pollock. In summer, 1996, juvenile sandlance and herring were non-selective and juvenile pink salmon were highly selective of prey. Prey selection among these species changed subtly from allopatric to sympatric aggregations. C) For herring and pollock, diets of allopatric

fish overlapped in summer and diets of sympatric fish overlapped in autumn. In summer, 1996, prey partitioning was indicated by low interspecific diet overlap between sympatric sandlance, herring and pink salmon and high diet overlap between allopatric species pairs. Intraspecific comparisons showed that sandlance shifted diets in the presence of other planktivores, but pink salmon and herring diets remained similar whether they occurred allopatrically or sympatrically.

9. The incidence of sympatry in PWS varied seasonally and among species. In 1994 after May, > 50% of sets that caught herring also caught pollock, and after July, > 50% of sets that caught pollock also caught herring. In July, 1996, juvenile herring, sandlance, and pink salmon (*Oncorhynchus gorbuscha*) occurred sympatrically in 21-41% of the hauls where at least one of the species was present.

Our results show that food webs in PWS are complex. Each of the three chapters of this report discussed particular aspects of forage fish feeding ecology. The prey suite available to fish in an area may change with time or may vary in different habitats; growth to larger body size may be accompanied by increased swimming speed and mouth gape, which facilitate predation on different taxa; increasing energy requirements may be more efficiently met by consuming larger items if the costs of consuming them are not too great; large, calorie-dense but nutrient-poor taxa may not meet fish nutritional requirements; diet overlap between species can shift seasonally based on ontogenetic prey requirements, fish movement patterns, and the timing of the onset of piscivory; forage fish interactions may be density dependent and depend on the incidence of sympatry; and interactions with other species may prompt shifts in prey consumption to avoid potential competition. Although shifts in diet may compensate to some degree, competitive interactions among forage species can result in reduced feeding. Energy may be the most important, but it is not the only currency. The nutritional requirements of forage species and the influences of different diets on their nutritional quality and growth are an area needing more intensive study. Diets of forage species may be adapted to their life history strategies. Lipid content was generally ranked highest for adult eulachon/lanternfish, second for herring, third for sandfish, sandlance and capelin, fourth for prowfish, and fifth for salmonids and gadids, and young fish generally had lower lipid content than larger/older fish (Roby et al, 1998). Since different zooplankters have different nutritional profiles, the nutritional quality of planktivorous forage species could be influenced by any of the diet attributes mentioned above. If sympatry occurs regularly under conditions of limited food availability, interspecific competition could affect the carrying capacity of PWS for these species. Density dependent effects have not been thoroughly examined. However, the migration of the majority of juvenile pink salmon to the Gulf of Alaska early in the summer reduces their interactions with other planktivorous forage fish in PWS. It is important to consider the frequency and duration of species co-occurrence to evaluate the importance of diet similarity and effects of trophic interactions. Our results indicate that planktivory is a factor that can determine the abundance of the preferred forage species of seabirds, but that careful consideration must be given to many factors, including sampling methodology, spatial and temporal distribution, allopatry vs. sympatry, school density, size distribution, prey availability, and oceanographic variations when evaluating results of diet analyses, and that directed sampling and perhaps manipulative studies are necessary to further elucidate the impacts of these variables. To further develop our understanding of the impacts of forage fish interactions and diet on their availability as seabird prey resources will require further studies with control for these factors.